Contributions of the maternal uterine environment and piglet genotype on weaning survivability potential: II. Piglet growth, lactation performance, milk composition, and piglet blood profiles during lactation following reciprocal embryo transfers between Meishan and White crossbred gilts[1]

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ABSTRACT: Crossbreeding studies between Meishan (MS) and Large White (LW) pigs have illustrated that increased piglet growth before weaning is attributed to the maternal genotype of LW dams. The objective of this study was to determine the contributions of the maternal uterine environment (MUE), piglet genotype (PigG), piglet age (PA), and their interactions on piglet growth, lactation performance, milk composition, and piglet blood profiles during lactation following reciprocal embryo transfers between MS and White crossbred (WC) gilts. Twenty-five successful pregnancies were generated by embryo transfer in 2 farrowing years representing all MUE × PigG combinations: MS × MS ($n = 4$ litters), MS × WC ($n = 7$ litters), WC × MS ($n = 7$ litters), and WC × WC ($n = 7$ litters). At d 1 and 10 and at weaning, piglets ($n = 147$, $n = 96$, and $n = 94$, respectively) were weighed and blood samples were collected and measured for hematocrit, hemoglobin, glucose, nitrogen, NEFA, albumin, lactate, and cortisol. In addition, sows were manually milked from a medial mammary gland to determine milk composition. All data were analyzed by ANOVA using MIXED model procedures with the fixed effects of MUE, PigG, PA, and their interactions. Piglet weight was greater ($P <$ 0.001) in piglets from WC dams compared to MS dams at d 10 and weaning but not at d 1. In addition, ADG were greater ($P < 0.05$) from piglets from WC dams compared to MS dams throughout lactation. However, milk composition was greater ($P < 0.05$) for GE and fat content from MS dams compared to WC dams, illustrating differences in milk quality between the breeds. There were significant MUE × PigG × PA interactions for hematocrit and hemoglobin levels in which greater ($P < 0.001$) levels were observed in MS piglets, irrespective of MUE, at d 1 of lactation and in MS piglets from MS dams at d 10 of lactation. Blood glucose was greater ($P = 0.01$) at d 1 in piglets from WC dams regardless of PigG but, at weaning, glucose was greater ($P = 0.01$) in WC piglets regardless of MUE. Serum NEFA levels were greater ($P = 0.02$) in piglets from MS dams throughout the lactation period. This study demonstrated that WC dams were superior to MS dams for piglet growth during lactation, in agreement with previous crossbreeding studies. However, blood components measured displayed complex interactions between the piglet and maternal breed, which signify possible mechanisms for improved preweaning survivability but slower lactational growth of MS piglets.

Key words: blood components, growth, lactation, piglet

Table 1. Number of litters and piglet observations for each maternal uterine environment (MUE) × piglet genotype (PigG) at d 1 and 10 and at weaning

MUE × PigG[1]	Litters, *n*	Piglet age		
		d 1	d 10	Weaning
MS × MS	4	25	16	16
MS × WC	7	34	21	21
WC × MS	7	36	22	22
WC × WC	7	51	37	35
Total	25	146	96	94

[1]MS = Meishan; WC = White crossbred.

INTRODUCTION

Piglet mortality affects approximately 13% of commercial piglets during lactation (PigCHAMP, 2010) and, therefore, significantly influences sow productivity (i.e., the number of pigs weaned in a given year). In contemporary western breeds, low birth weight piglets exhibit the greatest susceptibility to preweaning mortality (Damgaard et al., 2003; Tuchscherer et al., 2000). However, despite their lower birth weights compared to western breeds, Meishan (**MS**) piglets have lower preweaning mortality rates (Lee and Haley, 1995; Legault, 1985). The differences in mortality rates illustrate greater survivability of MS piglets, especially small weight piglets, that may be attributed to prenatal development of these piglets during gestation, thereby affecting early neonatal survival.

Crossbreeding studies between MS and Large White (**LW**) pigs have demonstrated that preweaning piglet survival is primarily attributed to the direct genotype in favor of MS piglets (Haley et al., 1995; Lee and Haley, 1995). In contrast, increased piglet growth before weaning was attributed to the maternal genotype in favor of LW dams (Bidanel et al., 1990). In our initial study (Miles et al., 2012) using reciprocal embryo transfer between MS and White crossbred (**WC**) gilts, we reported no significant interactions between the maternal uterine environment (**MUE**) and piglet genotype (**PigG**) on the development of early neonatal piglets (i.e., d 1 of age). This comparison demonstrated that MS piglets, regardless of uterine environment, have improved physiological development that enhances their early neonatal survivability (Miles et al., 2012) and, therefore, supports crossbreeding studies illustrating improved survival for MS piglets. Interactions between the MUE and PigG on subsequent piglet growth during lactation are unknown. Therefore, the objective of this study was to determine the contributions of the MUE, PigG, and their interactions on piglet growth, lactation performance, milk composition, and piglet blood profiles during lactation following reciprocal embryo transfer between MS and WC gilts.

MATERIALS AND METHODS

All animal protocols were approved by the U.S. Meat Animal Research Center Animal Care and Use Committee and met the USDA guidelines for the care and use of animals (USDA-ARS. 1990).

Animals

Piglets used for this study were born in 2 subsequent farrowing years (2007 and 2008) following reciprocal embryo transfers (**ET**) between MS and WC gilts. These ET produced 25 successful pregnancies corresponding to all possible MUE × PigG combinations (i.e., MS × MS [*n* = 4], MS × WC [*n* = 7], WC × MS [*n* = 7], and WC × WC (*n* = 7)]. Details regarding the genetics and maintenance of the dams, ET protocols, embryo donor and recipient data, litter statistics, and detailed physiological development of the neonatal piglets at d 1 of life can be found in our companion manuscript reporting the neonatal development (Miles et al., 2012). All surviving piglets from the companion study were used for the current study.

Piglet Growth

Approximately 24 h following parturition, litters were processed under normal management procedures (i.e., live-born piglets were weighed, sex was determined, tails were docked, and ears were notched) and stillbirth and mummified piglets were identified and recorded. Total litter size was based on recovery of all live and dead piglets (average 7.7 ± 1.6 number, mean ± SD) and did not differ between ET transfer groups (Miles et al., 2012). Piglets were weighed again at d 10 of age and at weaning (average weaning age = 17.9 ± 0.8 d, mean ± SD). Table 1 illustrates the number of litters and piglet observations for each MUE × PigG combination at d 1 and 10 and at weaning. The reduction in litter size from d 1 to 10 corresponded to humane removal of 46 piglets for the evaluation of physiological development reported in our companion manuscript. An additional 4 piglets were lost due to natural causes (i.e., crushed by the sow) throughout the lactation period. Average daily gain for each piglet was determined during early (d 1 to 10) and late (d 10 to weaning) lactation periodsand throughout the entire (d 1 to weaning) lactation period.

Lactation Performance and Milk Composition

Lactation performance of dams was estimated as nursed piglet weight gain (kg) during early (d 1 to 10) and late (d 10 to weaning) lactation periods and throughout the entire (d 1 to weaning) lactation period. For

determining milk composition, dams were given a 20 IU/mL intramuscular injection of oxytocin (RXV Products, Westlake, TX) to induce milk let down immediately before weighing and bleeding piglets at d 1 and 10 and at weaning. Approximately 15 min after oxytocin injection, dams were hand milked from medial mammary glands while piglets were kept off the sow. At each sampling (d 1 and 10 and weaning), approximately 15 mL of milk was collected from each sow and used to determine milk composition (i.e., DM, moisture, nitrogen, ash, and GE) using standard proximate analysis (AOAC, 1997). Milk lactose content was determined using an immobilized enzyme system (model 2700; Yellow Springs Instruments, Yellow Springs, OH). Milk fat content was estimated as a percentage of GE based on subtracting the percentage of protein content and lactose content from the GE.

Piglet Blood Profiles

Immediately after weighing piglets at d 1 and 10 and at weaning, all piglets were bled via jugular venipuncture using heparinized syringes. Blood was analyzed within an hour of collection for hemoglobin using a Hemoximeter (model OSM-2; Radiometer America, Westlake, OH) and hematocrits were determined using standard hematocrit tubes and centrifugation at 14,500 x g for 5 min at room tempurature. After measuring hemoglobin and hematocrit, blood was centrifuged at 2,000 × g for 10 min at 4°C and plasma was stored at –20°C. Plasma glucose, plasma urea nitrogen (**PUN**), and albumin were analyzed using the Technicon Autoanalyzer (Technicon Industrial Systems, Tarrytown, NY). For glucose, PUN, and albumin, samples were assayed in duplicate with intra-assay CV of 2.0, 0.7, and 2.3, respectively. Plasma NEFA concentrations were measured in duplicate using an enzymatic colorimetric method (Wako Pure Chemical Industries Ltd., Richmond, VA) with intra-assay CV of 5.4%. Plasma lactate was determined in duplicate using an immobilized enzyme system (model 2700; Yellow Springs Instruments) with intra-assay CV of 0.65%. Cortisol was measured using a commercial RIA kit (Diagnostic Systems Laboratories, Webster, TX) previously described and validated in swine (Wise et al., 2000). For cortisol concentrations, samples were measured in duplicate in 3 assays with an intra-assay and interassay CV of 8.3 and 9.7%, respectively.

Statistical Analysis

All data were analyzed using MIXED model procedures for ANOVA (SAS Inst. Inc., Cary, NC; Steel et al., 1997) and results are reported as least squares means ± SEM. The experimental unit for piglet measurements (i.e., piglet growth and piglet blood profiles) was the individual piglet and for sow measurements (i.e., lactation performance and milk composition) was the sow. When a significant *F*-statistic was generated, means were separated using a Dunnett multiple comparison test (SAS Inst. Inc.; Steel et al., 1997). Means were considered statistically different at $P < 0.05$ and tendencies between $P \geq 0.05$ and $P < 0.10$. Piglet weights and milk composition were analyzed with a model including the fixed effects of MUE, PigG, piglet age (**PA**) or lactation day (**LD**), farrowing year, and the interactions of fixed effects of MUE, PigG, and PA or LD; the covariate of litter size; and the random effect of sow within farrowing year × MUE × PigG interaction. Piglet ADG and lactation performance were broken into lactational periods (early, d 1 to 10; late, d 10 to weaning; and entire, d 1 to weaning) and analyzed separately with a model including the fixed effects of MUE, PigG, farrowing year, and the interactions of fixed effects and the random effect of sow within farrowing year × MUE × PigG interaction. Piglet blood profiles were analyzed with a model including the fixed effects of MUE, PigG, PA, farrowing year, and the interactions of fixed effects of MUE, PigG, and PA or LD; the covariate of litter size and d 1 piglet BW; and the random effect of sow within farrowing year × MUE × PigG interaction. Before statistical analysis, piglet BW, NEFA, lactate, and cortisol levels were log transformed to normalize the data and then back-transformed for reporting values.

RESULTS

Piglet Growth

Figure 1A illustrates piglet weights as the interaction between MUE, PigG, and PA. There was a significant ($P = 0.04$) MUE × PigG × PA interaction for piglet BW (Fig. 1A). At d 1 of age, piglet BW was less for MS piglets regardless of MUE and for WC piglets gestated in MS dams compared to WC piglets gestated in WC dams (Fig. 1A). By d 10 of age, piglet BW was less for MS piglets from MS dams compared to WC piglets from WC dams whereas piglet BW from the reciprocal ET treatment groups (i.e., MS × WC and WC × MS) displayed an immediate BW (Fig. 1A). However, by weaning, piglet BW was greater for piglets from WC dams compared to piglets from MS dams, irrespective of PigG (Fig. 1A). Figure 1B illustrates piglet ADG from the corresponding MUE by PigG treatment groups broken into lactational periods (early, d 1 to 10; late, d 10 to weaning; and entire, d 1 to weaning). During early lactation (i.e., d 1 to 10), ADG was greater ($P < 0.05$) in piglets from WC dams compared to piglets from MS dams (0.20 ± 0.01 vs. 0.14 ± 0.02 kg/d, respectively). During late lactation (i.e., d 10 to weaning),
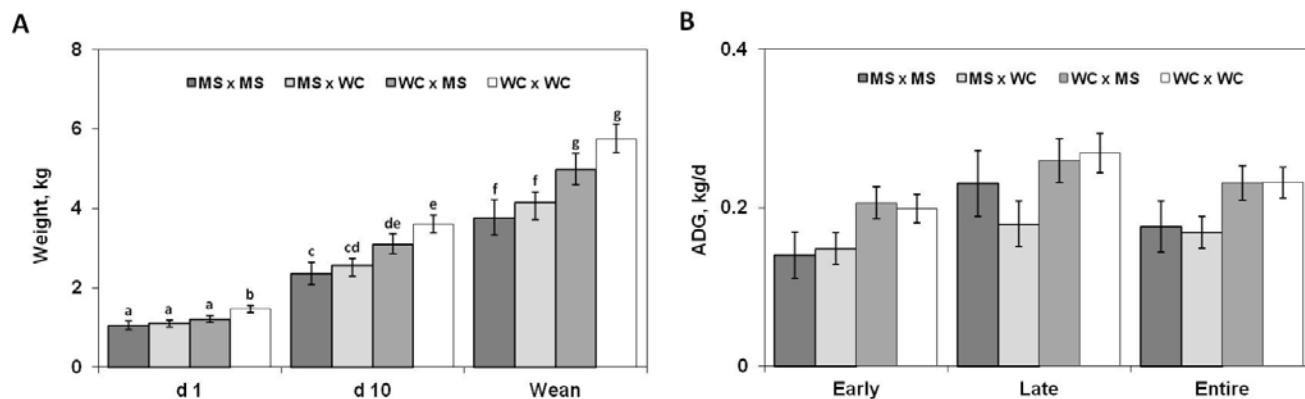
Figure 1. Piglet weights (Fig. 1A) illustrated as the interaction between maternal uterine environment (MUE), piglet genotype (PigG), and piglet age (PA). Piglet ADG (Fig. 1B) illustrated from the corresponding MUE by PigG treatment groups broken into lactational periods (early, d 1 to 10; late, d 10 to weaning; and entire, d 1 to weaning). The MUE by PigG combinations included the breed of the dam (Meishan [MS] or White crossbred [WC]) by the breed of the piglet (MS or WC). Piglet weight (Fig. 1A) had a significant MUE × PigG × PA interaction ($P = 0.04$). [a–g]Within PA for piglet weight, means separated by different superscripts are different ($P < 0.05$). Piglet ADG (Fig. 1B) was influenced by MUE ($P < 0.08$) main effect.

ADG tended ($P = 0.08$) to be greater in piglets from WC dams compared to piglets from MS dams (0.26 ± 0.02 vs. 0.20 ± 0.03 kg/d, respectively). Throughout the entire lactation (i.e., d 1 to weaning), ADG was greater ($P < 0.05$) in piglets from WC dams compared to piglets from MS dams (0.23 ± 0.01 vs. 0.17 ± 0.02 kg/d, respectively).

Lactation Performance and Milk Composition

Figure 2A illustrates dam lactation performance (i.e., nursed piglet weight gain) from the corresponding MUE by PigG treatment groups broken into lactational periods (early, d 1 to 10; late, d 10 to weaning; and entire, d 1 to weaning). During early lactation (i.e., d 1 to 10), lactation performance was greater ($P < 0.05$) in piglets from WC dams (1.90 ± 0.13 kg) compared to piglets from MS dams (1.44 ± 0.16 kg). During late lactation (i.e., d 10 to weaning), lactation performance did not differ between the treatment groups. Throughout the entire lactation (i.e., d 1 to weaning), lactation performance tended to be greater ($P = 0.07$) in piglets from WC dams (3.88 ± 0.33 kg) compared to piglets from MS dams (2.86 ± 0.40 kg). Figure 2B through 2F illustrate milk composition (i.e., DM, GE, protein, lactose, and fat content) as the interaction between MUE, PigG, and LD. There was a significant ($P < 0.001$) effect of LD on DM content of dam's milk, where DM progressively decreased as LD increased (25.5 ± 0.7, 22.2 ± 0.7, and $19.4 \pm 0.7\%$, respectively, for d 1 and 10 and weaning). Interestingly, MS dams had greater ($P = 0.02$) DM content in their milk ($23.4 \pm 0.6\%$) compared to WC dams ($21.3 \pm 0.5\%$), irrespective of PigG or LD. In addition, GE (Fig. 2C) of the milk was greater ($P < 0.05$) in MS dams (6.8 ± 0.1 kcal/g) compared to WC dams (6.3 ± 0.1 kcal/g), irrespective of PigG or LD. There was a significant ($P < 0.05$) PigG × LD interaction for

protein content (Fig. 2D) of the dam's milk. At d 1 of lactation, protein content of dams nursing WC piglets ($16.4 \pm 0.6\%$) was greater compared to dams nursing MS piglets ($13.2 \pm 0.8\%$). However, PigG did not affect protein content of dam's milk at d 10 and weaning. Lactose content (Fig. 2E) of dam's milk did not differ between MUE and PigG; however, lactose content was greater ($P < 0.001$) at d 10 ($19.2 \pm 1.3\%$) and weaning ($19.1 \pm 1.3\%$) compared to d 1 of lactation ($12.6 \pm 1.3\%$). Finally, fat content (Fig. 2F) of dam's milk was greater ($P = 0.01$) in MS dams ($62.9 \pm 1.9\%$) compared to WC dams ($56.2 \pm 1.5\%$), irrespective of PigG or LD.

Piglet Blood Profiles

Figures 3A through 3H illustrate piglet blood profiles (i.e., hematocrit, hemoglobin, glucose, PUN, NEFA, albumin, lactate, and cortisol) as the interaction between MUE, PigG, and PA. Hematocrit levels had a significant ($P < 0.001$) MUE × PigG × PA interaction. At d 1 of age, MS piglets from WC dams had the greater hematocrit compared to MS piglets from MS dams and WC piglets from MS dams whereas WC piglets from WC dams had significantly less hematocrit than the other MUE by PigG groups (Fig. 3A). By d 10 of age, hematocrit was greater in MS piglets from MS dams compared to WC piglets from MS dams, MS piglets from WC dams, and WC piglets from WC piglets (Fig. 3A). By weaning, hematocrit was not different between the MUE by PigG groups (Fig. 3A). Similar to hematocrit, hemoglobin levels were significantly ($P < 0.001$) affected by a MUE × PigG × PA interaction. At d 1 of age, MS piglets from WC dams had the greatest hemoglobin compared to MS piglets from MS dams and WC piglets from MS dams whereas WC piglets from WC dams had reduced hemoglobin compared to the other MUE by PigG groups (Fig. 3B). By d 10 age, hemo-
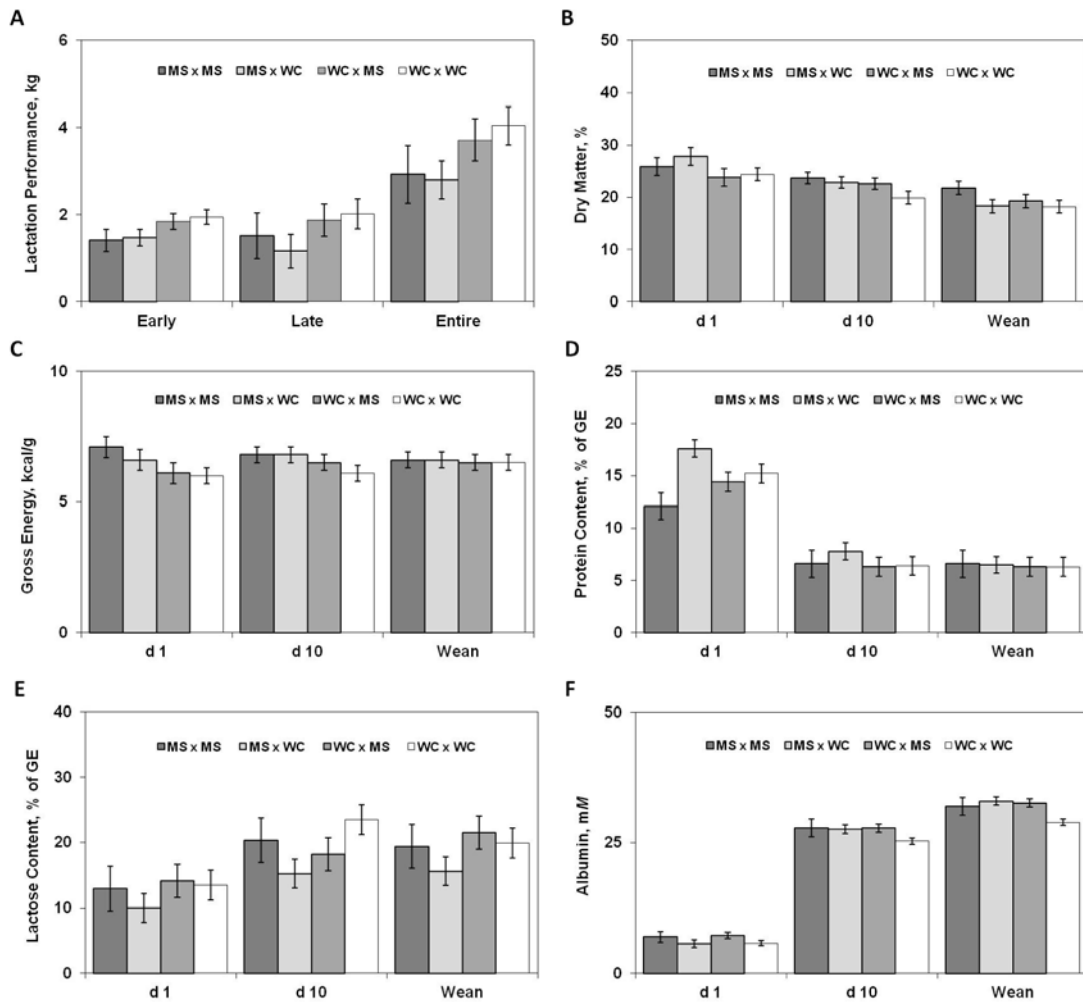
Figure 2. Dam lactation performance (Fig. 2A) illustrated as the interaction between maternal uterine environment (MUE) and piglet genotype (PigG) broken into lactational periods (early, d 1 to 10; late, d 10 to weaning; and entire, d 1 to weaning). Milk composition (Fig. 2B–2F) illustrated as the interaction between MUE, PigG, and lactation day (LD). The MUE by PigG combinations included the breed of the dam (Meishan [MS] or White crossbred [WC]) by the breed of the piglet (MS or WC). Dam lactation performance (Fig. 2A) was influenced by MUE ($P < 0.07$) main effects during early lactation and throughout the entire lactation. Dry matter content (Fig. 2B) of dam's milk also had MUE ($P = 0.02$) and LD ($P < 0.001$) main effects. Gross energy (Fig. 2C) of dam's milk was affected by a MUE ($P = 0.02$) main effect. There was a PigG × LD interaction ($P = 0.04$) for protein content (Fig. 2D) of dam's milk. Lactose content (Fig. 2E) of dam's milk was influenced by a LD ($P < 0.001$) main effect. Fat content (Fig. 2F) was affected by a MUE ($P = 0.01$) main effect.

globin was greater in MS piglets from MS dams compared to WC piglets from MS dams, MS piglets from WC dams, and WC piglets from WC dams (Fig. 3B). By weaning, hemoglobin was not different between the MUE by PigG groups (Fig. 3B).

There were significant MUE × PA ($P < 0.01$) and PigG × PA ($P < 0.01$) interactions for plasma glucose (Fig. 3C) levels in piglets. At d 1, piglets from MS dams had reduced glucose (4.3 ± 0.2 mM) compared to piglets from WC dams (5.1 ± 0.2 mM); however, by d 10 and weaning, there were no differences in glucose levels in piglets from MS and WC dams. In contrast, at d 1 and 10 of age, piglet glucose levels were similar in piglets from either MUE, but at weaning, WC piglets, irrespective of MUE, had greater glucose levels compared to MS piglets (6.6 ± 0.2 vs. 5.7 ± 0.3 mM, respectively). There was a significant PigG × PA ($P < 0.001$) interaction for PUN (Fig. 3D) levels in piglets.

At d 1 and 10 and at weaning, MS piglets had greater PUN levels (13.4 ± 0.8, 14.6 ± 1.0, and 12.6 ± 1.0 mM, respectively) compared to the corresponding WC piglets within each day (11.5 ± 0.5, 5.4 ± 0.6, and 4.6 ± 0.6 mM, respectively). Interestingly, piglet PUN levels remained similar in MS piglets throughout the sampling period whereas PUN levels decreased at d 10 and weaning in WC piglets compared to d 1. Piglet NEFA (Fig. 3E) levels were greater ($P < 0.05$) in piglets from MS dams (0.35 ± 0.03 mEq/L) compared to piglets from WC dams (0.28 ± 0.01 mEq/L), irrespective of PigG and PA. In addition, piglet NEFA levels were increased ($P < 0.001$) at d 1 and 10 (0.35 ± 0.02 and 0.36 ± 0.03 mEq/L, respectively) compared to weaning (0.24 ± 0.02 mEq/L), irrespective of MUE and PigG.

Piglet albumin (Fig. 3F) levels progressively increased ($P < 0.001$) with PA, irrespective of MUE or PigG (6.5 ± 0.4, 27.1 ± 0.5, and 31.6 ± 0.5 mM,
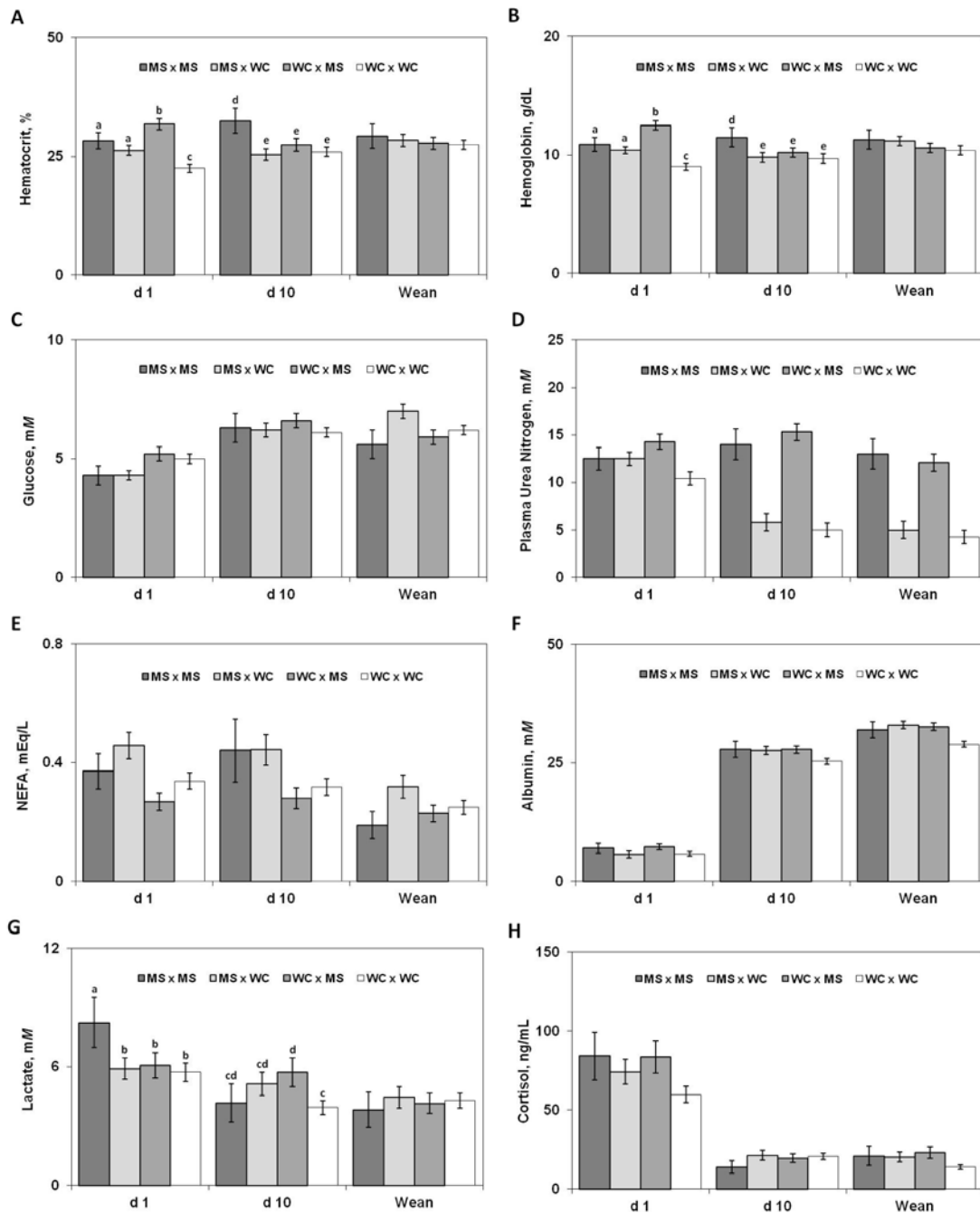
Figure 3. Piglet blood profiles illustrated as the interaction between maternal uterine environment (MUE), piglet genotype (PigG), and piglet age (PA). The MUE by PigG combinations included the breed of the dam (Meishan [MS] or White crossbred [WC]) by the breed of the piglet (MS or WC). Piglet hematocrit (Fig. 3A) and hemoglobin (Fig. 3B) levels were affected by a MUE × PigG × PA interaction ($P < 0.001$). Glucose (Fig. 3C) levels in piglets were influenced by MUE × PA and PigG × PA interactions (P = 0.01). Piglet plasma urea nitrogen (Fig. 3D) levels were affected by a PigG × PA interaction ($P < 0.001$). Piglet NEFA (Fig. 3E) levels were influenced by MUE ($P = 0.02$) and PA ($P < 0.001$). Albumin (Fig. 3F) levels in piglets were affected by a MUE × PigG interaction ($P = 0.05$) and a PA main effect ($P < 0.001$). There was a MUE × PigG × PA interaction ($P = 0.03$) for piglet lactate (Fig. 3G) levels. Piglet cortisol (Fig. 3H) levels were affected by a significant PA main effect ($P < 0.001$). [a–e]Within PA for piglet hematocrit, hemoglobin, and lactate, means separated by different superscripts are different ($P < 0.05$).

respectively, for d 1 and 10 and weaning). When averaging piglet albumin levels across 3 sampling days (d 1 and 10 and weaning), there was a significant ($P < 0.05$) MUE × PigG interaction for piglet albumin levels in which WC piglets from WC dams had reduced albumin levels (20.0 ± 0.4 mM) compared to the other MUE by PigG treatment groups (22.3 ± 0.9, 22.1 ± 0.5, and 22.5 ± 0.4 mM, respectively, for MS × MS, MS × WC, and

WC × MS). There was a significant ($P < 0.01$) MUE × PigG × PA interaction for piglet serum lactate (Fig. 3G) levels. At d 1 of age, piglet lactate was greater in MS piglets from MS dams compared to the other MUE by PigG treatment groups (Fig. 3G). By d 10 of age, piglet lactate had been reduced in MS piglets from MS dams such that they were similar to WC piglets from MS dams, MS piglets from WC dams, and WC piglets from WC

dams (Fig. 3G). However, at d 10 of age, piglet lactate was lower in WC piglets from WC dams compared to MS piglets from WC dams (Fig. 3G). By weaning, there were no significant differences in piglet lactate levels between the MUE by PigG treatment groups (Fig. 3G). Piglet cortisol (Fig. 3H) levels were only significantly (P < 0.001) affected by PA (74.8 ± 4.8, 18.5 ± 1.7, and 19.1 ± 1.8 ng/mL, respectively, for d 1 and 10 and weaning), irrespective of MUE or PigG.

DISCUSSION

Over the past 2 decades, selection for litter size in commercial swine herds has increased the number of pigs born alive; however, this increase has lead to a reduction in piglet birth weights, increased within-litter birth weight variability, and increased preweaning piglet mortality (Damgaard et al., 2003). Preweaning piglet mortality significantly limits sow productivity, which results in approximately US$600 million annual loss in profits for U.S. swine production. In addition to greater susceptibility to preweaning mortality (Damgaard et al., 2003), low birth weight piglets also grow slower after weaning compared to larger littermates (Wolter et al., 2002). Slower finishing growth of low birth weight piglets also influences the profitability of the swine industry due to greater feed costs and increased age to reach market weight. Contrary to contemporary western pig breeds, MS piglets weigh significantly less at birth but have reduced preweaning mortality rates (Lee and Haley, 1995; Legault, 1985). Our companion study (Miles et al., 2012) using reciprocal ET between MS and WC gilts demonstrated that d 1 MS piglets, regardless of MUE, have improved physiological development relating to oxygen-carrying capacities of the blood, appetite, activity, and energy stores that enhances their early neonatal survivability. Although the MS breed serves as a suitable model for studying preweaning survivability, MS pigs grow much slower and have lower mature weights compared to contemporary western pigs. Crossbreeding studies between MS and LW pigs have illustrated that increased piglet growth before weaning is attributed to the maternal genotype of LW sows (Bidanel et al., 1990). The current study investigated the contributions of the MUE, PigG, PA or LD, and their interactions on piglet growth, lactation performance of dams, and piglet blood profiles during lactation following reciprocal ET between MS and WC gilts.

There was a MUE × PigG × PA interaction for piglet BW. At d 1, WC piglets from WC dams were heavier than the other 3 treatment group (i.e., WC piglets from MS dams and MS piglets from both MS and WC dams), illustrating a suppressive effect of fetal growth within the MS uterine environment. A similar pattern

of fetal growth suppression by MS dams was observed in a previous study using reciprocal ET between MS and Yorkshire pigs (Wilson et al., 1998). Interestingly, in our companion study that analyzed only d 1 piglet BW, there was both a maternal and a piglet effect on the growth of piglets in which WC dams produced heavier piglets and WC piglets were also heavier than MS piglets (Miles et al., 2012). The discrepancy in these analyses likely resulted from the log transformation of the piglet BW in the current study to normalize the data across all days of lactation. By d 10, piglets from the reciprocal treatment groups (i.e., WC piglets from MS dams and MS piglets from WC dams) displayed immediate piglet BW compared to the within-breed treatment groups (i.e., MS piglets from MS dams and WC piglets from MS dams). However, by weaning, piglet BW was greater in piglets from WC dams, irrespective of PigG. Interestingly, there was a slight difference in ADG from early lactation (i.e., d 1 to 10) and late lactation (i.e., d 10 to weaning). Regardless, it is apparent that piglets from WC dams, irrespective of PigG, grew at a faster rate during lactation, as illustrated by increased ADG throughout the entire lactation period (i.e., d 1 to weaning). These findings on piglet growth support crossbreeding studies between MS and LW pigs demonstrating that piglet growth during lactation is primarily attributed to the maternal genotype in favor of LW sows (Bidanel et al., 1990).

Although the exact mechanism by which piglet growth is increased by WC dams is not known, it is likely that some component of lactation enhances piglet growth during this time period. This is further supported by a similar pattern of greater lactation performance as measured by nursed piglet weight gain during early lactation (i.e., d 1 to 10) and throughout lactation (i.e., d 1 to weaning) observed in WC dams irrespective of PigG. However, the milk composition of WC dams was not superior to that of MS dams in the current study. In fact, the composition of MS milk was greater in terms of GE and fat content compared to WC dams. The greater milk fat content from MS dams compared to WC dams in the current study was similar, as previously reported for early and late lactating MS and WC gilts (Alston-Mills et al., 2000). Unfortunately, the current study and a previously reported study (Alston-Mills et al., 2000) did not investigate total milk yield between these breeds; therefore, breed differences in milk quantity could explain increased lactational growth of piglets from WC dams compared to MS dams. In a study examining milk production and piglet performance in response to exposure to high ambient temperature, sows lactating in high ambient temperatures (29°C) had reduced milk yield compared to sows lactating in thermoneutral (20°C) environment (Renaudeau and Noblet, 2001). As

a results, piglet ADG and BW at weaning were reduced when nursed from sows in high ambient temperatures compared to thermoneutral temperatures (Renaudeau and Noblet, 2001). Interestingly, milk composition did not significantly differ in sows from the 2 environments, other than that DM and energy tended to be greater in milk from sows in high ambient temperatures (Renaudeau and Noblet, 2001). These results suggest that milk yield supersedes milk composition in terms of piglet performance. Follow-up studies are ongoing to determine breed influences on milk yield.

In the current study, milk lactose did not differ between the MUE and PigG but increased in later days of lactation (i.e., d 10 and weaning) compared to early lactation (i.e., d 1). The observed pattern of milk lactose composition was similar, as previously reported (Edwards and Hansen, 1996; Klobasa et al., 1987). Interestingly, there was a PigG × LD interaction for protein content of the dam's milk in which dam's nursing WC piglets had greater protein content compared to dam's nursing MS piglets at d 1 of lactation. However, no differences in protein content were observed at d 10 or weaning between the PigG and MUE. Protein levels drop dramatically in the pig as the colostrum produced immediately after farrowing changes to milk (Zou et al., 1992). The primary source of protein in sow colostrum is immunoglobulins, mainly IgG (Curtis and Bourne, 1971). As a result, the dramatic decrease in protein levels from colostrum to milk is driven by a significant drop in IgG as the colostrum changes to milk, which occurs before 24 h postfarrowing (Curtis and Bourne, 1971; Quesnel, 2011). The MS piglets could have nursed more vigorously and thus accelerated the transition from colostrum to milk, reducing the protein content in dam's milk. Evidence for this hypothesis are reported in our initial study (Miles et al., 2012), which demonstrated that MS piglets, irrespective of MUE, had greater stomach content at d 1 of life compared to WC piglets, thereby showing greater colostrum intake by MS piglets on the first day of life.

Complex interactions were observed in piglet blood profiles involved in oxygen carrying capacity, energy, and stress during the lactation period. A similar pattern for hematocrit and hemoglobin was observed when analyzing piglet profiles from all LD (d 1 and 10 and weaning) in the current study compared to analyzing only d 1 piglets in our companion study (Miles et al., 2012). These analyses illustrated that hematocrit and hemoglobin levels were elevated in d 1 MS piglets, irrespective of MUE, compared to WC piglets gestated in WC gilts. In addition, hematocrit and hemoglobin levels remained elevated in the MS piglets gestated in MS gilts through d 10 of life. Given hematocrit and hemoglobin involvement in ox-

ygen carrying capacity (Bucci, 2009), elevated levels of hematocrit and hemoglobin during early life in MS piglets likely benefits early neonatal survival.

Piglet plasma glucose levels displayed an interesting pattern for the MUE or PigG depending on PA. During the first day of life, piglets from MS dams had reduced glucose levels compared to piglets from WC dams, irrespective of PigG. A similar pattern of glucose levels was previously reported, illustrating reduced glucose levels in d 1 naturally bred MS piglets compared to WC commercial piglets (Mostyn et al., 2006). By weaning, WC piglets had greater blood glucose levels compared with MS piglets irrespective of MUE. Although the exact mechanisms for lower blood glucose in d 1 piglets gestated in MS dams and MS piglets at weaning is not known, this likely is a result in difference in nutrient partitioning from the more obese MS pigs compared to leaner commercial WC pigs.

Piglet PUN levels initially followed a similar pattern as hematocrit and hemoglobin at d 1 of life with MS piglets, irrespective of MUE, and WC piglets gestated in MS dams having greater levels compared to WC piglets gestated in WC dams. However, by d 10 and at weaning, MS piglets' PUN levels remained elevated compared to WC piglets irrespective of MUE. The difference in PUN at d 10 and weaning between MS and WC piglets likely reflects differences in protein utilization between the breeds. Plasma urea nitrogen levels are a good indicator of protein utilization in which low urea levels may be the result of reduced availability of ammonia caused by enhanced protein synthesis and reduced AA oxidation (Wu and Morris, 1998). White crossbreed piglets grew faster than MS piglets in the experiment, suggesting that AA would be incorporated into protein rather than deaminated (i.e., contributing to PUN) and further metabolized. This is likely to be the result of selection for growth rate in modern pig breeds compared to the MS.

Piglet NEFA levels were greater in piglets from MS dams, irrespective of PigG or PA. The difference in patterns of NEFA within piglet blood coincided with elevated levels of milk fat content between MS milk compared to WC milk and suggests that elevated NEFA was the result of greater fat in MS milk. A similar increase in NEFA levels was observed in young pigs fed a high-fat compared to a low-fat manufactured liquid diet, thereby illustrating a greater potential to accrue fat over protein due to an increased availability of fatty acids in young pigs consuming a high-fat diet (Oliver and Miles, 2010).

Piglet albumin levels increased from d 1 of life through d 10 and weaning, irrespective of MUE and PigG. This pattern has previously been reported and is due to the increasing synthesis of albumin by the liver (Ingvarsson et al., 1978). Plasma albumin levels are

indicative of the physiological maturation of the liver (Stone, 1984). Given that albumin levels were reduced in WC piglets from WC dams across the sampling period, these results suggest that MS piglets and some aspect of the MS dam improved liver maturation during late prenatal and early postnatal development. This is consistent with a previously reported pattern of increased albumin observed in pure-bred MS piglets compared to composite-line piglets and suggests that, despite their reduced size, MS piglets have greater maturation of the liver early in life (Herpin et al., 1993).

Piglet lactate levels were greater in MS piglets gestated in MS dams at d 1 of life compared to the other treatment groups. However, by d 10 of life, lactate levels dropped in MS piglets gestated in MS dams but remained elevated in MS piglets gestated in WC dams. Lactate is a key metabolite of anaerobic respiration and is known as an early marker of neonatal hypoxia (Skappak et al., 2013). This suggests that MS piglets from MS dams might be under aerobic stress during the first day of life. In addition, lactate can be used to synthesize endogenous glucose via gluconeogenesis (Adeva-Andany et al., 2014). As a result, this elevated lactate in MS piglets might be advantageous in maintaining glucose homeostasis during early life.

Finally, piglet cortisol levels differed only by PA, irrespective of MUE or PigG. Cortisol levels were elevated at d 1 of life and dropped to basal levels at d 10 and weaning. This pattern follows the classical pattern of cortisol following farrowing, consistent with the possible involvement of cortisol from the fetus on initiating and stimulating parturition (Randall et al., 1990).

In conclusion, this study demonstrated that piglet growth during lactation was influenced by maternal breed in favor of WC dams, which supports previous crossbreeding studies. However, blood components pertaining to survivability and growth displayed complex interactions between the piglet and maternal breed, which may signify possible mechanisms for improved preweaning survivability but slower lactational growth of MS piglets. Preweaning losses are greatest during the first days of life when capacity of piglets to consume milk is likely not limiting. During this time, MS dams produced milk with greater DM, GE, and fat content, thereby providing piglets with better nutrition, supported by higher NEFA in the blood of their piglets. Additionally, MS piglets have greater hematocrit and hemoglobin concentration during early life. Combined, these observations indicate that smaller MS piglets have greater potential to survive and that MS dams enhance this potential.

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